

AN ANALYSIS OF THE DEFENSIVE MECHANISMS OBSERVED IN
THE ANEMONE *ANTHOPLLEURA ELEGANTISSIMA* IN
RESPONSE TO ITS NUDIBRANCH PREDATOR
AEOLIDIA PAPILLOSA

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The sea anemone *Anthopleura elegantissima* (Brandt, 1835) is a conspicuous member of mid-intertidal communities along the exposed rocky west coast of the United States (Hand, 1955; Ricketts and Calvin, 1962; Sebens, 1977). Several recent studies (Waters, 1973; Harris, 1973; Edmunds, Potts, Swinfin and Walters, 1975, 1976) have reported that *A. elegantissima* is a preferred prey of the anemone-eating aeolid nudibranch, *Aeolidia papillosa* (Linnaeus, 1767). Edmunds *et al.*, (1976) described behavioral reactions of *A. elegantissima* to attack, including bulging of the column at the site of attack, crawling, and releasing from the substrate. Howe and Sheikh (1975) characterized an alarm pheromone, anthopleurine, from *A. elegantissima* and described the behavioral response it elicited in the anemone. Howe and Harris (1978) demonstrated that *A. papillosa* acquires anthopleurine when feeding on *A. elegantissima* and that leakage of the pheromone caused the alarm response in other individuals. Waters (1973) speculated that *A. papillosa* is evolving to specialize on *A. elegantissima*.

Anthopleura elegantissima has well-developed behavioral responses to attack by *A. papillosa*, but none of these behaviors provides an effective defense in the laboratory. In addition, *A. papillosa* is consistently found associated with one of its least preferred prey, the subtidal anemone *Metridium senile* (Linnaeus, 1767) (Harris, 1973; Brewer, 1977). The ineffectiveness of the defenses of *A. elegantissima* against one of its chief predators under laboratory conditions and the fact that the predator is primarily associated with a less preferred prey suggests that the defenses may be more effective under natural conditions. The purpose of this study was to investigate a series of potential defensive mechanisms which may provide at least partial protection for *A. elegantissima* against *A. papillosa*. The effectiveness of these mechanisms were then evaluated in the context of the environment in which this predator-prey association is found.

MATERIALS AND METHODS

This study was conducted during the period of January to June 1976, though L.G.H. had been making observations on *A. papillosa* since 1964. The laboratory experiments and observations were conducted at the facilities of Hopkins Marine Laboratory, Pacific Grove, California. Field studies were done at the laboratory and at two nearby locations in Monterey Bay (36° 37' N, 121° 53' W).

Some of the specimens of *Anthopleura elegantissima* were collected from a rock

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outcropping on the east side of the laboratory and adjacent to a ramp for an old boat works (Site 1). These rocks face east and are exposed to direct sunlight from sunrise to late afternoon (1500–1600 hr). Most of the specimens of *Anthopleura elegantissima* and some of the specimens of *Aeolidia papillosa* were collected from the rocky intertidal zone under abandoned sardine canneries (Site II) located adjacent to the laboratory; this site is shaded by the buildings and only receives direct sunlight from sunrise until about 1200 hr. Most of the specimens of *A. papillosa* were obtained from a subtidal site under Wharf No. 2 in Monterey (Site III). At this site, specimens of *A. papillosa* of various sizes can be obtained throughout the year, feeding on the large concentrations of *Metridium senile* (Yarnall, 1972; Brewer, 1977). Animals were maintained in running sea water at ambient temperatures (14° C).

It is important to distinguish between two forms of *Anthopleura elegantissima* present in Monterey Bay and farther south. The clonal form of *A. elegantissima* is restricted to the midtide zone, forms clones by binary fission on open rock surfaces, and seldom grows to a column diameter greater than 50 mm. A solitary form of *A. elegantissima* is found in the lower intertidal zone and to depths of 15 m; it attaches in cracks in the rock substrate and has not been observed to reproduce asexually. Individuals of this anemone may attain a column diameter of greater than 80 mm. In this study, we will refer only to the clonal form.

Intensive surveys of two rocky intertidal sites (Sites 1 and II) were undertaken in March and again in May, 1976, to determine densities of *A. papillosa* associated with *A. elegantissima*. Site II under the canneries faced northeast and received direct sunlight only during the morning hours. Small specimens of *A. papillosa* were common among clones of *A. elegantissima* at this site from January through March, 1976. Sampling was done using a 1.64-m quadrat to determine the relative density of *A. papillosa* compared to the density of *A. elegantissima*. No specimens of *A. papillosa* were ever found associated with clones of *A. elegantissima* at Site I, so no quadrat sampling was done there nor at Site II in June.

Three experiments were conducted to assess the importance of desiccation as an environmental stress on *A. papillosa*. In the first, six specimens of *A. papillosa* and six specimens of *A. elegantissima* were placed in stacking dishes without water for 6 hr. The experiment was done in the laboratory to approximate the time of exposure at neap low tide on a sunless day. In the second and third experiments, groups of *A. papillosa* were placed on rocks among clones of *A. elegantissima* immediately after the water had receded below the clones and were retrieved just prior to reflooding by the incoming tide. At the end of each experiment, animals were placed in dishes containing fresh sea water and held for 24 hr. Those animals which were moribund or unable to hold onto the glass dish after 24 hr were considered lost, while those which were attached and crawling normally were rated as surviving the low tide. The justification was that animals which were too weak to remain attached to the rock would be washed free by wave action. A nudibranch washed off a rock in the midtide may ultimately survive, but it is at least removed from the anemones on which it had been feeding. Controls were left in running sea water during the experiments.

Observations were made on feeding encounters between *A. elegantissima* and *A. papillosa* to determine the sequence of attack, the behavioral responses of *A.*

elegantissima and the preference of *A. papillosa* for particular regions of the anemone. In the first experiment, a number of anemones were removed from rocks and placed in a dish coated with silicone grease which prohibited their attachment. These anemones were left in running sea water for 24 hr and at the time of the experiment a majority of them were open. Fifty nudibranchs (body length 2–3 cm) were released into the dish and allowed to feed for 5 hours. To determine sites of attack by *A. papillosa*, the anemones were then relaxed in 7% MgCl (in fresh water) and surveyed for tissue damage which was obvious by direct observation. In a second experiment, approximately 100 specimens of *A. elegantissima* from a single clone were placed in a running sea-water table and groups of four to five nudibranchs were placed among the anemones; attacks were described and tabulated.

Observations showed that contact of any part of the nudibranch with the column of an anemone caused local swelling of the column at the site of contact. Preliminary experiments showed that the anemones were responding to *A. papillosa* mucus. A series of experiments were conducted to determine the site of receptivity of *A. elegantissima* to *A. papillosa* mucus, the duration of the response and the specificity of this response relative to other nudibranch species.

The tentacles or the column of the anemones were touched with mucus-covered or blank cotton swabs in the first experiment. In experiment two, mucus was obtained from the back or the foot of *A. papillosa*, from the aeolid *Hermisenda crassicornis* (Eschscholtz, 1831) and from the dorid nudibranch *Anisodoris nobilis* (Odhner, 1907). *A. nobilis*, which eats only sponges, served as a control in the second set of experiments. In all tests, nudibranchs were rubbed with a wet cotton swab which was then applied to a part of the body of the anemone. A separate swab was used for each anemone. The behavior of the anemones and duration of any response was described from observations made several times an hour.

RESULTS AND OBSERVATIONS

Qualitative sampling of a number of exposed rocky intertidal habitats along the California coast by both authors over several years showed that *A. papillosa* is found in association with clones of *A. elegantissima* throughout the year. The density of nudibranchs tends to be higher in the winter than in the summer, and a majority of the animals seen and/or collected were large—between 30 and 80 mm in length.

At certain times of the year, *A. papillosa* can be very common in association with *A. elegantissima* (Table I). Small specimens of *A. papillosa* (mean length 12 mm; maximum 22 mm) were prevalent at the canneries site (Site II) from January through March. However, the mean length of animals observed and/or collected did not increase over this 3-month period, and they were not present a few hundred meters away at Site I. In late April, a storm pounded the intertidal zone with approximately 2.5-m waves. From late April through July no specimens of *A. papillosa* were observed at either of the intertidal stations, although at Site III all sizes were common in subtidal fouling communities (Table I). *A. papillosa* grows from 1 mm to over 30 mm in about 2 months when feeding on *A. elegantissima* in the laboratory (Harris, in preparation); this suggests that

TABLE I

Comparison of *Aeolidia papillosa* density in association with anemone clones at two intertidal and one subtidal (8 m) sites in Monterey Bay in winter and summer. Site I is a rocky outcropping on the beach on the NE side of Hopkins Marine Station. Site II is a rocky ledge under the canneries about 300 m E of Site I. Site III is under commercial Wharf No. 2 in Monterey. Site I and II contain clones of *Anthopleura elegantissima* and Site III is dominated by clones of *Metridium senile*. Where no quadrat numbers are given, a minimum of 5 hr of observations were made at each site during that month.

Number <i>A. papillosa</i> /m ² of anemone clone				
Site	February 1976	April 1976	June 1976	Time of direct exposure to sunlight
I	0 m ²	0	0	sunrise to ~1600. sunrise to ~1200.
II	24.3/m ² (104 1/64 m ²)	0	0	
III	86 m ² (10 1/10 m ²)	present	9.5 m ² (20 1/10 m ²)	none

nudibranchs were continuously recruiting to the site under the canneries but that they were not surviving long enough to reach sexual maturity.

Small specimens of *A. papillosa* (< 15 mm length) were typically found within 2 cm of the anemones. Often this was at the edge of a clone or within a scattered aggregate of anemones. A nudibranch might be in a small depression or crack in the rock surface, but the majority of individuals were exposed on flat surfaces, apparently having made no attempt to hide when the tide receded. Large specimens of *A. papillosa* (> 15 mm) may be found farther from their prey and typically seek out cracks in which to hide when not feeding. However, even with intensive

TABLE II

A summary of quadrat analyses done to assess the relative density of *Aeolidia papillosa* in relation to the percentage of free space among *Anthopleura elegantissima* clones. The sampling was done at Station II under the canneries on 12 February 1976. The quadrat size was 1/64 m², and 104 quadrats were sampled.

% Free space	0%	25%	50%	75%	Total
Number of quadrats	22	39	31	12	104
Number of quadrats with <i>A. papillosa</i>	2	17	11	4	34
Number of <i>A. papillosa</i>	2	18	18	5	44
					Mean
Number of <i>A. papillosa</i> per quadrat	0.09 ¹	0.46	0.56	0.41	0.42
Density of <i>A. papillosa</i> per m ² of <i>A. elegantissima</i> clone	5.8	29.4	35.8	26.2	24.3
% Quadrats with <i>A. papillosa</i>	9%	43%	35%	33%	33%

¹ Significant at <0.01 (*t*-test).

TABLE III

Results of desiccation experiments in which *Aeolidia papillosa* was exposed to air for 6 hr and then returned to fresh sea water. Survival was determined after 24 hr. Experiment 1 was done in the laboratory while experiments 2 and 3 were conducted in the field by placing nudibranchs adjacent to clones of *Anthopleura elegantissima* on the receding tide and retrieving them just prior to submergence on the incoming tide. The results were significant at less than 0.01% using chi square.

Experiment	1	2	3A	3B
Number of <i>A. papillosa</i>	6	10	32	33
Number surviving after 24 hr (%)	4 (66%)	4 (40%)	16 (50%)	13 (39%) ¹
Control survival	100%	100%	100%	100%

¹ Eighteen nudibranchs disappeared when the tide washed over the rock containing the animals before they could be retrieved; only 15 animals remained and the 18 missing *A. papillosa* were considered killed.

searching, no nudibranchs larger than 22 mm were found at Site II during the period from January through June 1976.

Results of the quadrat sampling at Site II illustrate the tendency of small nudibranchs to be found in open areas adjacent to groups of *A. elegantissima* (Table II). The quadrats were only placed over areas containing *A. elegantissima*, because numerous observations indicated that *A. papillosa* remains close to its prey. Only two nudibranchs were found within what appeared to be solid masses of anemones while the vast majority occurred at the periphery of clones. Close examination revealed that even in the most tightly packed clones, there was usually bare rock between pedal disks. The sampling data suggest that anemones within tightly packed clones are essentially free from predation by *A. papillosa*. While *A. papillosa* tended to be found at the periphery of clones where there is more free space, two other predators or parasites, the prosobranch *Epitonium tinctum* (Carpenter, 1864) and the pycnogonid *Pycnogonum stearnsi* (Ives, 1892) were common only within these tightly packed aggregations.

While no individuals of *A. papillosa* were collected at Sites I and II during the late spring and summer of 1976, one of us (L.G.H.) had previously collected specimens of *A. papillosa* and egg masses at several locations (Eagle Point, San Juan Islands, Washington; Dillon Beach and Bodega Bay, California) during the months of June and July. These sites are more exposed open coastal locations than the protected environment of Monterey Bay. In each case, the density of *A. papillosa* was well below 1/m² of *A. elegantissima* clone. The majority of the nudibranchs were large (> 40 mm), sexually mature, and were located in tidepools or at the lower end of the anemone's distribution in the intertidal.

Results of tests on the effects of desiccation on *A. papillosa* are recorded in Table III. In both the laboratory and the field experiments, survival of test animals exposed to air for 6 hr was approximately 50%, while control animals maintained in running sea water had 100% survival. In the initial laboratory test, two animals died even though they were sitting in small amounts of residual water and mucus. Most of the nudibranchs were still reactive after 6 hr out of water, but those that ultimately died were unable to hold onto the dish after water was added.

Two smaller nudibranchs (about 20 mm) set out at Site I were so desiccated that they had to be scraped from the rock surface.

In Experiment 3B, (see Table III), 33 specimens of *A. papillosa* were placed among a clone of *A. elegantissima* at Site II. Due to a miscalculation, the nudibranchs were not retrieved until after a few small swells had already washed over the area. Only 15 out of the 33 animals were still attached to the rocks; the other

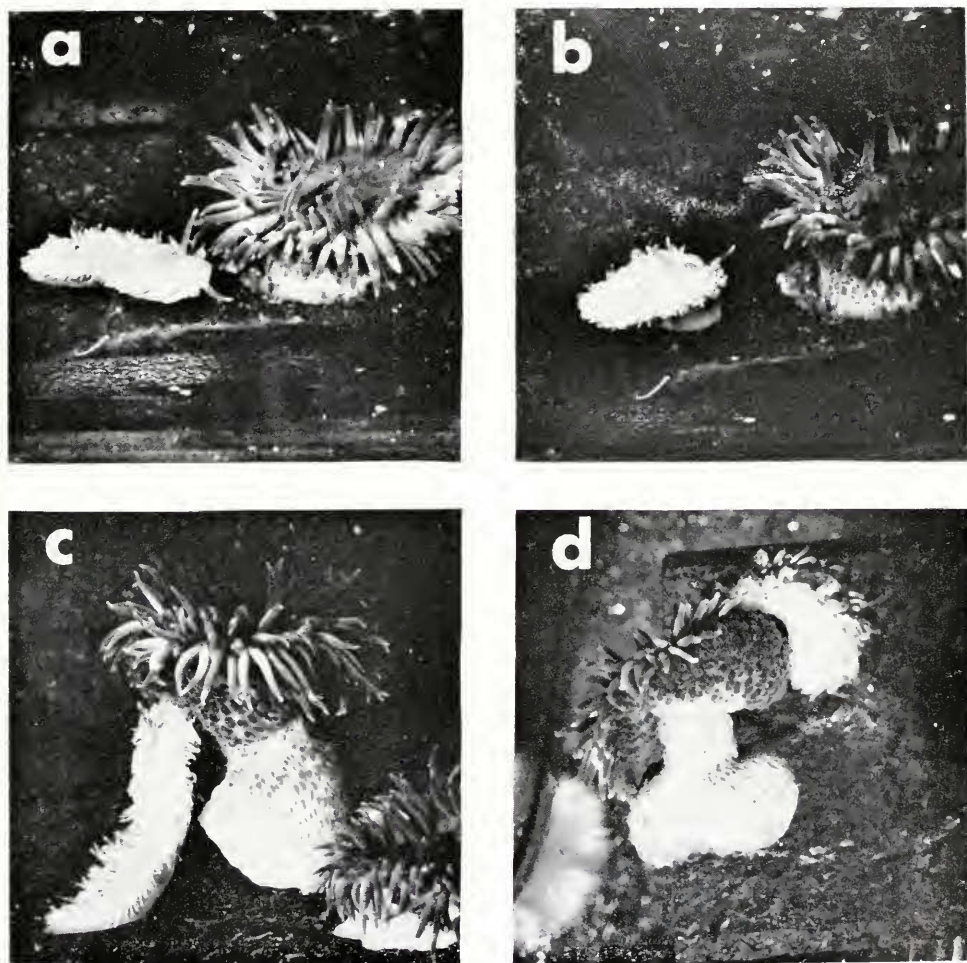


FIGURE 1. Photographic illustration of the initial contact between specimens of *A. papillosa* and *A. elegantissima* and two resulting feeding behaviors and anemone responses: (a) the initial contact involving the nudibranch's rhinophores and the anemone's tentacles; (b) the mutual retraction that typically occurs following first contact; (c) this nudibranch fed on the column for about 3 hr and made numerous attempts to reach the tentacles which were out of reach due to bulging of the column; (d) this nudibranch reached the tentacles before bulging of the column began and was lifted free of the substrate. The nudibranch fed in this position for about 3 hr; note line of mucus and detritus on the glass left by the anemone as it crawled during the attack.

TABLE IV

Feeding experiments to determine whether *Aeolidia papillosa* shows a preference for specific body regions when attacking *Anthopleura elegantissima*. In Experiment A the anemones were not attached and were lying on their sides so an approaching nudibranch had one chance to encounter the oral area first, two chances for the column and one chance for the pedal disk. In Experiment B, the anemones were attached and a nudibranch would typically make contact with a tentacle first, but then it would touch the column even if it attacked the tentacles. The results were significant at less than 0.01% using chi square.

Experiment	A		B	
	Predicted (%)	Actual (%)	Predicted (%)	Actual (%)
Column	16.5 (50%)	4 (12%)	30.5 (50%)	19 (31%)
Tentacles	8.25 (25%)	18 (54%)	30.5 (50%)	42 (69%)
Pedal disk	8.25 (25%)	11 (33%)	0 ¹	0

¹ Anemones were attached so pedal disk was not available.

18 animals had disappeared, presumably washed away by slight swells (about 30 cm). Of the 15 animals remaining, 13 survived.

The results of a separate experiment also suggest the unsuitability of the intertidal for *A. papillosa* in the late spring and summer. On 2 May, 1976, 18 small specimens of *A. papillosa* (mean size 15 mm) were placed among marked clones in protected habitats under the canneries. The animals were placed among clones where there were cracks and algae to provide refuges from desiccation. Three days later, only one nudibranch could still be found in the area where it was placed. By the eighth day, no specimens of *A. papillosa* remained in the vicinity. During the late spring and summer this protected habitat, which is shaded after 1200 hr is apparently too stressful for *A. papillosa*.

The behavior of the nudibranch attack and anemone responses have been described previously (Russell, 1942; Waters, 1973; Harris, 1973; Edmunds *et al.*, 1976), but they will be reviewed because it is relevant to understanding the mechanism behind the bulging behavior described by Edmunds *et al.*, (1976). Figure 1 illustrates the sequence of attack. Initial contact is typically between the nudibranch's rhinophores and the anemone's tentacles (Fig. 1a). The tentacles and nudibranch both retract (Fig. 1b). *A. papillosa* then moves into attack with buccal mass extended, rhinophores retracted and cerata bristled. The oral tentacles touch the column causing it to bulge in the area touched (Figs. 1c, d). The bulging behavior consists of an exaggerated relaxation of the column wall where contact has been made. Waves of contraction run up and down the column and changes in height and shape are frequent during bulging. This behavior continues for up to 6 hr after a single contact with *A. papillosa* mucus. A result of this behavior is to raise the tentacles out of reach of the nudibranch (Fig. 1c). If the *A. papillosa* does reach the tentacles, before bulging is initiated, it may be lifted free of the substrate (Fig. 1d).

Experiments testing for a preferred site of feeding by *A. papillosa* on *A. elegantissima* showed that the tentacles are selected over the column (Table IV). Nudibranchs also select the pedal disc over the column when anemones are not

attached. This preference for the tentacles is even more obvious when the attack sequence is observed; as in Figure 1c, nudibranchs often finally fed on the column, because the anemone's behavioral responses prevented easy access to the tentacles.

The bulging behavior of *A. elegantissima* is elicited by mucus from *A. papillosa* and also from the aeolid *Hermisenda crassicornis* which occasionally attacks anemones (Table V). That mucus from *A. papillosa* caused bulging was first indicated during attempts to observe the alarm response in a tidepool containing several anemones. An *A. papillosa* was placed in the pool to determine if feeding on one anemone would cause the alarm response in other individuals. The nudibranch crawled between two anemones, but did not attack either. Within minutes the contacted anemones had elongated their columns; they remained in this expanded and distinctive posture for over 2 hr. This indicated to us that mucus from the nudibranch may be initiating this behavior. Subsequent experiments (Table V) verified this hypothesis. Mucus from *A. papillosa* caused the column to bulge, and this behavior pattern lasted for 3 to 6 or more hours even without further stimuli from the nudibranch. In addition to inflation of the column on the side touched, the verrucae dropped their attached sand grains and shell bits.

Tests conducted to determine sites of sensitivity in *A. elegantissima* to *A. papillosa* mucus revealed that only the column was responsive. The tentacles contracted when touched by mucus, but did not elicit any inflation behavior by any part of the column and returned to their normal relaxed position within a minute or two. Howe and Sheikh (1975) showed that the tentacles were the site of greatest sensitivity to the alarm pheromone anthopleurine. Mucus from any part of *A. papillosa* and from *Hermisenda crassicornis* elicited column bulging, while mucus from *Anisodoris nobilis* had no observable effect on anemone behavior. Some anemones continued to show bulging reactions for 6 or more hours after a single contact with mucus from *A. papillosa* even in running sea water. Since 6 hr is the approximate time of submergence during a tidal cycle and *A. papillosa* only feeds during high tide, these results suggest a two-part mechanism in which anthopleurine causes a quick and short-term contraction of the tentacles which increases the likelihood that *A. papillosa* will contact the column first. Contact with the column will result in mucus from the nudibranch being

TABLE V

Summary of two experiments to test the effects of *Aeolidia papillosa* mucus on column bulging in *Anthopleura elegantissima*. Mucus secreted from glands on the foot and on the cerata was compared. Mucus from two other nudibranchs was also used; *Hermisenda crassicornis* occasionally attacks anemones, while *Anisodoris nobilis* eats only sponges and served as a control.

Source of Mucus	% Anemones bulging over time in minutes						
	0	min 60	120	180	240	300	360
<i>A. papillosa</i> foot (34) ¹	0%	76	62	53	29	18	6
<i>A. papillosa</i> cerata (37)	0%	81	84	81	62	32	22
<i>H. crassicornis</i> (37)	0%	65	84	78	51	24	22
<i>A. nobilis</i> (40)	0%	2.5	5	7.5	7.5	2.5	0

¹ Total number of anemones used in two replicate experiments.

sensed by the column receptors; this will initiate a slow but long-lasting inflation of the column that will raise the tentacles far above the substrate, often out of reach of the nudibranch.

Verification that *A. papillosa* mucus elicits bulging under field conditions occurred during desiccation experiment 3 (Table III). Nudibranchs were placed in clear areas within scattered clones. Water and mucus from the nudibranchs drained down the rock surfaces and around anemones below the nudibranchs. Thirty minutes after the experiment began, anemones which contacted the fluid draining from *A. papillosa* were bulging; many dropped their sand grain cover and several had released from the rock. The unattached anemones were lying on their sides with the column bulged, but the slope was too gentle for them to fall or roll from their original position without water movement. The next day the anemones were reattached, contracted and recovered with sand grains. However, comparison of photographs taken during the experiment and the following day showed that a number of anemones had moved 2 to 6 cm and four anemones had disappeared.

When attacked by *A. papillosa*, individuals of *A. elegantissima* crawl in the opposite direction. In 3 hr animals may have crawled as far as 4 cm. In the next 24 hr animals continued to crawl for another 3 to 4 cm, although limited observations suggest that in the field they may not crawl as far as they do in the laboratory.

In the laboratory, approximately 10% of the anemones attacked by *A. papillosa* released from the substrate during the attack. We do not know whether the percentage of release is as high in the field where there is active water movement, though both authors have encountered *A. papillosa* in tide pools in the process of attacking unattached anemones. Verrucae of detached anemones are extremely adhesive and attach quickly to any object that they contact. Unless there is active water movement at the time anemone releases, it may ultimately reattach in the same area.

DISCUSSION

The clonal form of *Anthopleura elegantissima* occurs primarily in the midtide zone on the exposed coastline of the west coast of North America (Hand, 1955; Ricketts and Calvin, 1962; Dayton, 1971; Francis, 1973a, b; Sebens, 1977). In this habitat individuals are exposed to wave action and six or more hours of exposure to air twice every 24 hr. Connell (1972) has suggested that the upper limit of a species in the intertidal is due to physical factors, especially physiological tolerance to exposure, and that the lower limits are due primarily to biological factors such as competition and predation. Dayton (1971) showed that *A. elegantissima* cannot survive in more protected areas of the San Juan Islands, because it is incapable of withstanding the long mid-day low tides in the summer. The exposure experiments (Table III) and collecting data suggest that specimens of *A. papillosa* are less able to withstand desiccation than their prey and that affects their ability to hold on to the substrate when the tide returns. The effect of desiccation appears to be greatest in the warmer months of the year and in protected areas such as Monterey Bay, since *A. papillosa* can be collected with *A. elegantissima* in the summer at exposed, open coastal sites (Waters, 1973).

A. papillosa presumably survives better in exposed habitats because spray from waves decreases the threat of desiccation.

The majority of large, reproductive *A. papillosa* found associated with clones of *A. elegantissima* have been at the lower end of the anemone's range in the intertidal. The mean size of *A. elegantissima* is greatest in these habitats (Sebens, 1977). Sebens (1977) has suggested that the longer submersion time increases feeding time for the anemones. A similar phenomenon has been described for the gastropod *Tegula funebris* (Paine, 1969). The largest specimens of *T. funebris* were found in the lower intertidal where the increased food supply and time for feeding would be translated into greater reproductive output. However, this was offset by increased threat of predation by the starfish *Pisaster ochraceus*. It is likely that the intertidal distribution of *A. elegantissima* represents at least a partial or seasonal refuge from predation by *A. papillosa* and that the lower limit of the anemone's range is influenced by where the balance between the potential for increased reproductive output and the threat of predation comes out in favor of predation.

Clone formation in *A. elegantissima* has been described as a competitive strategy that allows for rapid space utilization (Sebens, 1977). The fact that *A. elegantissima* has a well developed aggressive response to encroachment by other anemones similar to that reported for corals by Lang (1973) reinforces the likelihood that clone formation is an adaptation for space competition (Francis, 1975b, 1976; Purcell, 1977). Clone formation may also have adaptive significance as a defense against predation. Veligers of *A. papillosa* settle on the rock surface adjacent to their anemone prey (Harris, unpublished observations); therefore, only the periphery of a clone will be available for recruitment of the predator. The circumference of a clone of anemones is less than the sum of the circumferences of the same number of individual anemones were they dispersed, so there is less surface area for settlement. Also, the anemones at the center of the clone will be relatively free from predation (Table II) while those at the periphery of the clone will be exposed to the greatest damage from nudibranch attacks.

Francis (1976) has shown that anemones at the periphery of a clone serve as soliders which expend most of their energy in the production of nematocysts and regenerating wounded areas after aggressive encounters. These soldiers do not contribute directly to asexual or sexual reproductive efforts of the clone. Assuming that clone formation is primarily a competitive strategy similar to encrusting colonial growth as proposed by Jackson (1977), the additional adaptive value of minimizing the threat of predation for a majority of clone-mates should have a synergistic effect in reinforcing selection for cloning.

A. papillosa shows a clear preference for the tentacles of *A. elegantissima* (Table IV). The final feeding site is dependent on several factors including relative sizes of the predator and prey, the initial position of the tentacles, and the reaction of the anemone. If the length of the nudibranch is equal to or greater than the column diameter of the anemone, then the aeolid is large enough to readily attack the tentacles of an anemone in the normal open position (see Fig. 1a). Should the tentacles be raised in an alarm response or chance behavior, then the likelihood of the nudibranch reaching the tentacles is reduced, particularly if the anemone responds to contact with the column by bulging (Figs. 1c, d).

A. papillosa that have previously eaten *A. elegantissima* leak anthopleurine for up to 7 days and anthopleurine leaked from a nudibranch will initiate the alarm response (Howe and Harris, 1978). The alarm response, which involves a quick general contraction of the tentacles, may be of some advantage to an anemone in that it does increase the possibility that *A. papillosa* will not contact the tentacles first. A number of encounters have been observed in which the nudibranch gave up when it failed to reach the tentacles of an anemone. A specimen of *A. papillosa* feeds daily and primarily at high tide. The response to anthopleurine leaking from a nearby nudibranch should be greatest at the beginning of a high tide, since the anemones will have been free of the water-carried signal during low tide; continued exposure to anthopleurine causes fatiguing of the response over time (Howe and Sheikh, 1975).

The alarm response is of short duration and therefore not likely to deter a large, persistent nudibranch. However, raising the tentacles does increase the likelihood that the predator will touch the column. The column responds to *A. papillosa* mucus by swelling and this behavior pattern lasts for several hours (Table V).

There are two possible advantages to bulging behavior. The first is protection of the tentacles. It should be selectively advantageous to keep the feeding structures intact and instead to lose tissue from the column. Attacks to the column typically involve removal of epidermal tissue which will be regenerated, and very seldom result in complete penetration of the body wall. The second advantage is that when a specimen of *A. papillosa* attempts to reach or succeeds in reaching the tentacles, it must release at least partially from the rock surface (Figs. 1c, d) and will be vulnerable to being dislodged by wave action. Being washed off the rock by surge may not kill the nudibranch, but it removes it from further predation on the same clone.

The site of reception for the water-transmitted pheromone, anthopleurine, is the tentacles of *A. elegantissima*, and the alarm response involves short duration, generalized contraction of the tentacles (Howe and Sheikh, 1975). *Acolidia papillosa* mucus is detected by contact, the receptors are in the column and the response is a localized inflation of the column. It is predictable that the receptors for a water-transmitted pheromone would be in the tentacles, for they extend farthest from the central axis of the animal. The generalized alarm response should be most effective if it occurs before contact is made with the predator since no directionality of response is required. It also seems likely that the receptors for a localized response to a slow-moving predator would be at the site of the response as is the case with the receptors for the bulging behavior.

Crawling by an anemone after an attack will potentially decrease the likelihood of a second attack because of the presence of the other members of the clone. Nudibranchs attack the first individual they encounter when foraging. This would spread the damage produced by a nudibranch to several members of a clone and decrease the chances for the loss of an individual and shrinkage of the clone. Another effect of crawling behavior would be to isolate the nudibranch on the rock substrate, increasing the chances of desiccation. This is most likely to occur in young nudibranchs that do not show a strong tendency to hide at low tide.

Approximately 10% of the encounters observed in the laboratory between *A. papillosa* and *A. elegantissima* resulted in the anemone releasing from the substrate. Rosin (1969) reported a similar escape response in *Anthopleura nigrescens* (Verrill) to its predator, the aeolid nudibranch *Herziella* sp. In the field, detaching from the rock substrate will potentially result in the anemone being carried to new habitats which may be viewed as a means of dispersal of the clone, and therefore, a positive side result of this association.

A specimen of *A. papillosa* consumes 50 to 100% of its wet body weight each time it feeds, which is at least once a day (Howe and Harris, 1978). Therefore, the nudibranch becomes an increasing threat as it grows to a point where it is capable of killing an anemone in a single meal; this suggests that the selective value of the defensive mechanisms discussed would be most effective against young nudibranchs. *A. papillosa* is about 0.5 mm in length when it first metamorphoses. Nudibranchs about 1 mm in length grow to about 35 mm and become sexually mature in a little over two months in the laboratory (Harris, in preparation). This suggests that the time and size must be considered in evaluating the selective value of defensive mechanisms since it will be at least 2 months after metamorphosis before a nudibranch is able to cause serious damage during an encounter or before it begins to reproduce.

None of the defensive adaptations described in this paper stop *A. papillosa* veligers from metamorphosing in a clone, nor are they effective in deterring predation in any given encounter between a nudibranch and an anemone either in the field or in the laboratory. We suggest that these mechanisms interact in such a way that the predator is killed before it reaches sexual maturity. The overall defensive strategy seems to be to minimize damage to clone members and to increase the likelihood that the predator will be killed or removed by desiccation and/or wave action.

The best evidence for this proposed defensive strategy is the fact that *A. papillosa* is primarily associated with the subtidal anemone *Metridium senile* (Harris, 1973, 1976, and in preparation). A similar pattern occurs in the Atlantic where *A. papillosa* is associated with *Metridium senile* (Stehouwer, 1952), *Sagartia elegans* (C. Todd, University of North Wales, personal communication) and *Cercus pedunculatus* (J. Tardy, University of Poitiers, personal communication); these three anemones were found to be among the least preferred in laboratory studies by Edmunds *et al.* (1975). Swennen (1961) reported large numbers of specimens of *A. papillosa* feeding on *Actinia equina*, a preferred species found in a similar habitat to that of *Anthopleura elegantissima*. Swennen's observations were made during the winter when the threat of desiccation would be least.

To influence the prey preference hierarchy of *A. papillosa*, the defensive strategies of anemones should focus on preventing the nudibranch from reaching sexual maturity and reproducing. Young nudibranchs seldom leave the prey where they have metamorphosed unless the prey is consumed or the nudibranch attains sexual maturity and searches for a mate (Harris, 1973); therefore, the choice of initial prey species takes place at the veliger stage prior to metamorphosis. The primary criterion for the choice of prey species must be survival to sexual maturity and reproduction. The prey preferences reported in the literature (Waters, 1973; Harris, 1973; Edmunds, *et al.*, 1975) are derived from laboratory

choice experiments with adult nudibranchs. Harris (1976) proposed that the prey preference hierarchy for the veliger stage of *A. papillosa* should be limited to relatively few species of anemone in an area and the principle criterion for selection should be survival to reproduction. In contrast, adult nudibranchs should be much less selective in their choice of prey since continued survival and reproduction should be the primary consideration at this stage. *A. papillosa* attains sexual maturity 2 to 3 months after metamorphosis and at a length of about 35 mm; an individual nudibranch is capable of continuing to reproduce for 6 or more months while growing to about 120 mm (Swennen, 1961; Harris, 1973; Clark, 1975). Adult specimens of *A. papillosa* show ingestive conditioning to even non-preferred anemones and will seek out prey they are conditioned to, unless they make contact with a more preferred species, and then they will switch (Harris, 1973; Wood, 1968; Murdoch, 1969). A hungry specimen of *A. papillosa* will attempt to feed on virtually any anemone species and even the corallamorpharian *Corynactis californica* Carlgren, 1936 (Waters, 1973; Harris, in preparation; Edmunds *et al.*, 1975).

In conclusion, the clonal form of *Anthopleura elegantissima* has evolved a series of defensive mechanisms including intertidal position, cloning, the alarm response to the pheromone, anthopleurine, column bulging initiated by nudibranch mucus, crawling and releasing from the substrate. None of these adaptations prevent veligers of *A. papillosa* from metamorphosing in association with *A. elegantissima* nor do they prevent an attack. However, they do combine in the context of the natural environment to form a very effective defensive strategy which increases the chances that the predator will be removed and/or killed by desiccation and/or wave action before it grows to sexual maturity. By preventing reproduction in the majority of nudibranchs which do metamorphose on this species, *A. elegantissima* exerts negative selective pressure on the prey preference hierarchy of the veliger stage. The success of this defensive strategy is illustrated by the fact that *A. papillosa* is primarily associated with one of the least preferred anemones of adult *A. papillosa*.

Mechanisms like cloning and the release of anthopleurine may also serve other functions such as competition or communication between clonemates. The fact that these mechanisms have adaptive value for more than one aspect of the anemone's biology should increase the selection for these traits.

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SUMMARY

1. The defensive mechanisms shown by the west coast, intertidal sea anemone, *Anthopleura elegantissima*, in response to its nudibranch predator *Acolidia*

papillosa are identified and evaluated in the context of the environment where *A. elegantissima* occurs. The defensive mechanisms include intertidal distribution, clone formation, alarm response, bulging of the column, crawling and releasing from the substrate.

2. *A. papillosa* are primarily located at the periphery of clones so that anemones in the interior of the clone have a refuge from predation. Assuming that cloning is an adaptation for space competition in *A. elegantissima*, then the additional advantage derived as a defensive mechanism should increase selection for clone formation.

3. *A. papillosa* was less able than *A. elegantissima* to withstand desiccation from exposure at low tide. This suggests that the intertidal distribution of *A. elegantissima* is a defensive adaptation which reduces the threat of predation by *A. papillosa* at least during the warmer months of the year.

4. The bulging of the column at the site of contact was found to be a localized response of several hours duration. The mucus of *A. papillosa* stimulated the response and the receptors were found to be situated in the column. Mucus from the coelenterate-eating aeolid nudibranch, *Hermisenda crassicornis*, also initiated the response while neither the mucus from the sponge eating dorid, *Anisodoris nobilis*, nor control swabs dipped in sea water caused bulging.

5. None of the defensive mechanism directly protects an anemone from attack by *A. papillosa*. The defensive mechanisms all interact to minimize damage to the clone until the predator is removed by desiccation and or wave action. This strategy is most effective during the 2- to 3-month period between when the veliger metamorphoses and when the nudibranch reaches sexual maturity.

6. This defensive strategy of killing the young nudibranch before it reproduces may negatively influence prey selection by the veliger stage. The evolution of the prey preference hierarchy of the veliger stage should be based on the criterion of survival to sexual maturity. Evidence for the effectiveness of this defensive strategy is that *Aeolidia papillosa* is primarily associated with the subtidal anemone, *Metridium senile*, one of the least preferred prey of adult nudibranchs.

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